DEMOGRAPHIC COMPOSITION OF IMMATURE GREEN TURTLES (CHELONIA MYDAS) FROM THE EAST CENTRAL FLORIDA COAST: EVIDENCE FROM mtDNA MARKERS

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ABSTRACT: Green turtles are highly migratory and difficult to study in aquatic habitats. Despite much progress in recent decades, some aspects of the green turtle's life history remain obscure. Long distance migrations by adults between foraging grounds and nesting habitats are striking, yet juvenile movements are poorly known. We performed mixed-stock analysis using mtDNA markers on a foraging population of juvenile green sea turtles, *Chelonia mydas*, from Hutchinson Island, Florida, to determine the origin of these animals. The results indicate that contributions to this population from previously surveyed nesting populations were 53% from Costa Rica, 42% from the United States and Mexico, and 4% from Aves Island (Venezuela) and Surinam. Results differed significantly from a similar juvenile foraging population in the nearby Bahamas (Costa Rica: 80%; United States and Mexico: 5%; Aves Island and Surinam: 14%; Ascension Island and Guinea Bissau: 1%). This difference may be due to a number of factors resulting in geographic or temporal changes in haplotype composition. Results of this study reinforce the need for cooperative international management of migratory species.

 $\textit{Key words}: \;\;\; \text{Foraging population; Mixed-stock analysis; Migration; Life history; Neritic environment}$

MARINE turtle movements are difficult to study due to their aquatic migratory routes, vast geographic scale, and the animals' occupancy of multiple coastal and pelagic habitats during different developmental stages. The geographic location and duration of developmental stages are probably species specific, but the general life history model initially proposed by Carr et al. (1978) applies to most turtle species. Although highly adapted for an aquatic lifestyle, females come ashore to lay eggs. Upon emergence from their nests, hatchling turtles enter the ocean engaging in a swimming frenzy that may exceed 24 h (Carr and Ogren, 1960; Deraniyagala, 1939). Thus begins a lifetime of migratory behavior, both passive (Carr and Meylan, 1980) and active, which carries them through different developmental habitats.

During the first decade(s) of their lives, the various species of marine turtles begin to depart from the generalized life history proposed by Carr et al. (1978). For example, the flatback turtle, *Natator depressus*, apparently does not have a pelagic

stage and movements are limited to the continental shelf of Australia (Miller, 1997). In contrast, both Atlantic and Pacific loggerhead turtles, *Caretta caretta*, have an extended pelagic stage, make transoceanic migrations (Bolten et al., 1998; Bowen et al., 1995) and pass through several developmental habitats before returning to nest at their natal beaches. In comparison to loggerhead turtles, the pelagic stage of green turtles may be shorter in duration since recruitment to neritic developmental habitats generally occurs at a smaller size (Musick and Limpus, 1997).

Immature green turtles (Chelonia mydas) are found along the Florida east coast in nearshore waters (Ernest et al., 1989; Guseman and Ehrhart, 1990; Martin et al., 1989) and inland lagoons and estuaries (Ehrhart, 1983; Mendonça, 1983; Mendonça and Ehrhart, 1982; Witherington and Ehrhart, 1989). Historically, immature green turtles were abundant and commercially harvested from the Indian River Lagoon system (True, 1887; Wilcox, 1898; Witzell, 1994). Adult green turtles occur

relatively infrequently in these coastal waters, and green turtle nesting occurs in low numbers along the Florida coast (Dodd, 1982; Ehrhart and Raymond, 1987; Meylan et al., 1995; Proffitt et al., 1986; Williams-Walls et al., 1983). Because immature sea turtles are known to occur 100s or 1000s of kilometers from their natal beaches, several nesting populations, such as those in Costa Rica, Aves Island, and Mexico, could contribute individuals to the Florida foraging population.

Tagging studies provide information on movements of individual turtles over discreet periods, defined by the longevity of the marker (Chaloupka and Musick, 1997). Much information on reproduction in adult females has been generated through the use of externally applied tags (Carr et al., 1978). However, due to an initial small size and high rates of mortality, hatchlings cannot realistically be tracked with external tags over their lifetime; therefore, the origin of juveniles at particular foraging locations cannot be determined using conventional methods.

Mitochondrial (mt) DNA markers in conjunction with mixed stock analysis (MSA) have proven useful in examining the demographic composition of marine turtle foraging populations (Broderick et al., 1994). Mixed stock analysis was originally applied in studies of fish populations in the northwest Pacific to examine the impact and effectiveness of hatchery programs (Grant et al., 1980). This analysis employs a maximum likelihood approach for estimating the relative contributions of source populations or stocks to a potentially mixed population (Pella and Milner, 1987). Marine turtle foraging sites have been shown to consist of animals from multiple nesting populations, and MSA has successfully been used to estimate the relative contributions of regional nesting locations to these sites (Bass, 1999). Foraging sites are believed to be important developmental habitats, and molecular markers recently have been used to document shifts in the demographic composition of turtles in these habitats (Laurent et al., 1998). Several different foraging locations of Chelonia mydas have been examined including both juvenile and adult populations in the Caribbean (Bass et al., 1998; Lahanas et al., 1998). This paper extends existing surveys of West Atlantic foraging populations to include immature green turtles from the east central coast of Florida.

Knowledge of the genetic composition of marine turtle foraging populations can provide vital information for guiding management strategies. Do the individuals in this east central Florida foraging location originate from one nesting population or multiple nesting populations? Furthermore, elucidating factors that influence recruitment to developmental habitats may generate testable predictions about movements during different stages of a species' life history. For example, is recruitment to the nearshore developmental habitat a random process or are there other factors that determine the relative contributions to a regional foraging population such as the one in Florida?

MATERIALS AND METHODS

Marine turtles are routinely captured in the large submerged intake pipes that collect cooling water at the St. Lucie power plant on Hutchinson Island, Florida (Ernest et al., 1989; Martin et al., 1989; Proffitt et al., 1986). The power plant intake pipes are located about 365 m offshore at a depth of 7 m and lead to a 1500-m intake canal in which the turtles become entrained. This entrainment yields an unusual opportunity to sample animals that would otherwise require a resource intensive sampling regime. The turtles are examined, tagged to prevent resampling, and returned to the ocean. The mean straightline (notch-to-notch) carapace length of the 62 green turtles sampled was 44.4 cm (SD = 12.4 cm; range 25.0-70.1 cm), andthe mean mass was 12.8 kg (SD = 11.3 kg; range 2.2–45.8 kg). Blood samples, initially intended for hormonal analyses, were collected from 62 green turtles between 3 February 1992 and 23 May 1994. The red blood cells were stored at -20 C. In 1996, the red blood cells were transferred to lysis buffer (100 mM Tris-HCl, 100 mM EDTA, 10 mM NaCl, 1% SDS; pH 8.0) and stored at room temperature.

We conducted DNA isolations using a standard phenol/chloroform method (Hillis et al., 1996). Approximately 300 µl of blood in lysis buffer was incubated with 1X STE buffer, 20% SDS, and 10 mg/ml proteinase K at 65 C for 2 h. A 510-bp fragment of the mtDNA control region was amplified with the PCR method (Mullis and Faloona, 1987) using primers LTCM-1 and HDCM-1 (Allard et al., 1994). The cycling thermal parameters used were as follows: 1 cycle at 94 C (1 min) followed by 35 cycles at 94 C (45 s), 55 C (30 s), and 72 C (45 s), and finally a 3-min extension at 72 C. Standard precautions, including negative controls (template-free PCR reactions), were used to test for contamination and to assure the fidelity of the PCR reactions (Innis et al., 1990).

Cycle sequencing reactions with fluorescently labeled dideoxynucleotides were conducted in the DNA Sequencing Core at the University of Florida. Sequencing products were analyzed with an automated DNA sequencer (Applied Biosystems model 373A) at the aforementioned facility. Sequences were aligned using an exhaustive search-and-compare algorithm in the program Sequencher (v.3.0, Gene Codes Corporation). Visual inspection and removal of unnecessary gaps prevented misalignments. Polymorphic sites were identified and used to match haplotypes to those observed at nesting locations [n =194 individuals surveyed by Encalada et al. (1996) and Lahanas et al. (1998)]. The green turtle rookeries previously surveyed in the Atlantic and Mediterranean are located at Ascension Island (U.K.), Atol das Rocas (Brazil), Aves Island (Venezuela), Florida (U.S.A.), Lara Bay (Cyprus), Matapica (Surinam), Pailoa (Guinea Bissau), Quintana Roo (Mexico), and Tortuguero (Costa Rica). Sequences that matched known haplotypes were collated for analysis whereas unique haplotypes were resequenced in the opposite direction to assure the accuracy of haplotype designations. Sequences that did not match known haplotypes were amplified and sequenced a second time to confirm their uniqueness. Percent sequence divergence was calculated for new haplotypes using the Kimura 2-parameter model with an 8.5:1 (transition:transversion) ratio (Encalada et al., 1996) in the GenDist program of PHYLIP (Felsenstein, 1993). To determine the possible source populations of new haplotypes, a phylogenetic tree was generated using the neighbor-joining algorithm with an Australian haplotype as the putative outgroup (Encalada et al., 1996). Bootstrap estimates were generated using 1000 replicates.

In the original nine nesting populations surveyed, haplotype frequencies were tested for homogeneity (Encalada et al., 1996). Of the 36 pairwise tests conducted, three were not statistically different from each other: United States versus Mexico; Ascension Island versus Guinea Bissau; and Aves Island versus Surinam. Consequently, samples from these locations are pooled into regional population units for Chi-square and mixed stock analyses.

To test for statistical differences among haplotype frequencies at rookeries and foraging areas, we performed Chi-square analyses with the program CHIRXC (Zaykin and Pudovkin, 1993), and probabilities were generated using a Monte Carlo randomization procedure (Roff and Bentzen, 1989). To correct for simultaneous tests, we applied the highly conservative sequential Bonferroni technique (Rice, 1989) to the probabilities generated by CHIRXC. Relative contributions of the surveyed Atlantic-Mediterranean green turtle rookeries were estimated using the programs GIRLSEM and UCON (Masuda et al., 1991). GIRLSEM uses an iteratively reweighted least squares algorithm to compute the conditional maximum likelihood estimate of composition by comparing the haplotype frequencies in the source populations (nesting colonies) and the mixed population (foraging ground). UCON computes an unconditional estimate. Both analyses are subject to sampling errors of type composition in the stocks and mixture. A major assumption of both methods is that all potential source populations have been included in the analyses. Standard deviations were calculated using the infinitesimal jackknife procedure in GIR-LSEM and UCON.

We assessed hypotheses concerning the contributions of nesting populations using Chi-square tests. In addition, linear regression models with two potentially important variables, rookery size (both minimum and maximum estimates) and distance (from rookery to foraging location), were also tested. Variables were transformed into arcsine values, and both maximum and minimum population size estimates were used in the models. Distances (expressed in nautical miles) were calculated using the program Geographic Distances (Legendre and Vaudor, 1991), which computes distances between locations following the earth's curvature. When two distant populations were pooled for the MSA, the average distance was used as the corresponding distance variable for the pooled populations in the regression analysis.

RESULTS

Of the 62 blood samples sequenced, 61 matched known haplotypes. Forty-three of the individuals carried haplotype CM III, a common haplotype found at several western Atlantic green turtle rookeries, including Quintana Roo, Florida, Tortuguero, and Aves Island. Twelve individuals carried haplotype CM I, found in individuals from Florida and Quintana Roo. Three individuals carried haplotype CM V found at rookeries in Quintana Roo, Aves Island, and Matapica. Two individuals carried haplotype CM XVIII found only at the Quintana Roo nesting location, and one individual carried haplotype CM II found only in Florida. The remaining haplotype, hereafter referred to as CM XXII, did not match any of the known haplotypes from the original analyses of Caribbean green turtle nesting or foraging locations (Encalada et al., 1996; Lahanas et al., 1998). Neighbor-joining analysis (Fig. 1) was performed to determine the phylogenetic affinity of haplotype CM XXII. The results indicated that this haplotype was most similar to eastern Caribbean haplotypes. There are several possible ex-

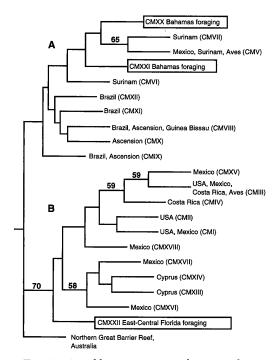


FIG. 1.—Neighbor-joining tree showing relationships between haplotypes and rookeries and the position of haplotype CMXXII relative to previously identified haplotypes from Encalada et al. (1996) and Lahanas et al. (1998). The "A" group consists of haplotypes found primarily in eastern Caribbean rookeries and the "B" group consists of haplotypes found in western Caribbean rookeries. Nodes with values greater than 50% bootstrap support are indicated.

planations for the origin of this haplotype. It may have come from an unsurveyed nesting location or it could exist in low (undetected) frequency at one of the surveyed nesting locations. It was not included in the mixed stock analyses.

Chi-square analyses indicated that the haplotype frequencies of the foraging area were significantly different from the haplotype frequencies at all surveyed nesting locations (P < 0.05), which statistically removes the possibility that all surveyed juveniles came from a single nesting colony. The haplotype frequencies from two foraging locations previously examined in the Caribbean, Bahamas (Lahanas et al., 1998) and Nicaragua (Bass et al., 1998), were also tested for homogeneity. The sample from east central Florida was significantly different from both the juvenile foraging

TABLE 1.—Maximum-Likelihood (ML) estimates of the composition of east central Florida juvenile green turtles from the programs GIRLSEM and UCON (assuming equal contributions from source populations as a starting point for ML iterations). Estimates are expressed as a proportion (±1 SD) of the foraging ground sample.

	GIRLSEM	UCON	
Source population	Contribution		
U.S./Mexico	$0.4237 (\pm 0.0950)$	$0.4238 (\pm 0.0934)$	
Costa Rica	$0.5344 (\pm 0.0934)$ $0.5346 (\pm 0.092)$		
Aves/Surinam	$0.0418 (\pm 0.0301)$ $0.0415 (\pm 0.030)$		
Brazil	0		
Ascension/Guinea Bissau	0 0		
Cyprus	0		

group in the Bahamas (n=80; $\chi^2=19.89$, P<0.001) and the adult foraging group represented by samples from the Nicaraguan green turtle harvest (n=60; $\chi^2=17.24$, P<0.001).

The first null hypothesis, that all sampled nesting locations contribute with equal probability, was tested with UCON and GIRLSEM. Both analyses indicated

that three of the six potential source populations contribute to the population of animals captured at Hutchinson Island (Table 1, Fig. 2). To estimate the relative contributions of the Florida and Quintana Roo nesting samples, a second ML analysis was conducted treating these nesting sites as separate source populations (Table 2). Although the haplotype frequencies of

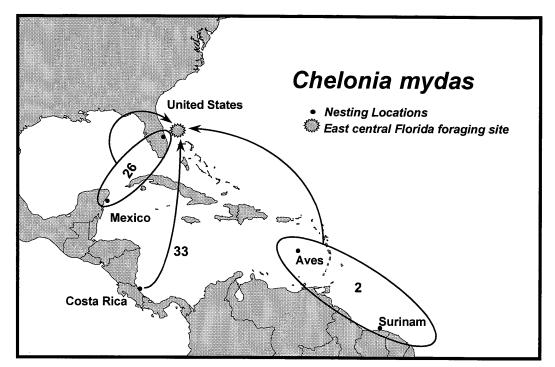


FIG. 2.—Map of green turtle (*Chelonia mydas*) nesting locations relative to sampled foraging population off the east central Florida coast. Ellipses indicate that individuals from these nesting locations were pooled for the maximum likelihood analysis. The estimated number of individuals (in sample examined) contributed to the foraging population are indicated. Several nesting populations are not shown due to scale and no indication of contribution (see text for complete listing of nesting populations in the Atlantic and Mediterranean).

TABLE 2.—Results of GIRLSEM analysis excluding source populations that did not contribute in the initial analysis. In addition, two populations combined in the initial analysis (Florida and Mexico) were separated and treated as independent source populations. Estimates are expressed as a proportion (±1 SD) of the foraging ground sample.

Source population	Contribution	SD
United States	0.3719	± 0.1170
Mexico	0.0936	± 0.0606
Costa Rica	0.4869	± 0.1054
Aves/Surinam	0.0474	± 0.0300

nesting females from Florida and Quintana Roo were not significantly different from each other (P=0.031), this determination of non-significance was based upon a highly conservative correction, the sequential Bonferroni technique. In addition, the Quintana Roo nesting population contains several "endemic" haplotypes, and there is no evidence of movement of tagged females between these locations.

The hypotheses concerning the proportion of nesting populations contributing to the foraging area were examined using adjusted Chi-square tests. Only those populations that were indicated by the ML analysis to contribute to the foraging area were used. In these tests, results were compared to (1) expected values based on

equal contributions from the three nesting groups and (2) expected values based on population sizes for the three nesting groups (Table 3). The hypothesis predicting that populations have an equal probability of contributing individuals to the foraging area was rejected ($\chi^2 = 18.177$; P <0.005). The second hypothesis that populations contribute in proportion to their size was also rejected (minimum size: χ^2 = 39.26; P < 0.001; maximum size: $\chi^2 =$ 31.31, P < 0.001). Linear regression models including all populations used in the analysis indicated that distance was a significant determinant of the percent contribution by a particular rookery [P > t]0.04 (min size of population) and P > t =0.03 (max size of population)], whereas the size of the population was not a significant determinant P > t = 0.21 (min size of population) and P > t = 0.11 (max size of population)].

DISCUSSION

Comparison to Other Foraging Grounds

Comparing the estimates of contributions to different juvenile and adult green turtle foraging grounds may provide insights into the mechanisms that govern recruitment and determine migratory routes in this species. There are significant dif-

Table 3.—Expected contributions to Florida foraging ground based on two hypotheses concerning the factors important in determining the composition of foraging ground populations. H_1 represents expected contributions based on the number of nesting females at each location divided by the total number of nesters. H_2 assumes an equal probability of contributions from the three source populations. H_1 and H_2 were examined using adjusted Chi-square tests. Where estimated numbers of females nesting per year is given as a range, the minimum and maximum estimates were used and both expected values were tested. Estimates of population size compiled from Encalada et al. (1996) and Lahanas et al. (1998). Estimates of rookery size and distances (nautical miles) were used in the linear regression analysis.

Nesting location	Rookery size estimated No. females/year	Distance (nm)	H _i : Rookery size expected contribution	H ₂ : Equal contribution expected contribution	ML estimate observed contribu- tion
Aves Isl., Venezuela	300-500	1147	0.2306-0.0835	0.1667	0.0418
Matapica, Surinam	2000	1903			
Tortuguero, Costa Rica	5000-23,000	1034	0.5013 - 0.7686	0.1667	0.5344
Atol das Rocas, Brazil	50-100	3308	0.0050 - 0.0033	0.1667	0.0000
Ascension Isl., U.K.	1600-3000	4336	0.2005 – 0.1136	0.1667	0.0000
Guinea Bissau	400	3771			
Lara Bay, Cyprus	100	2444	0.0100 - 0.0033	0.1667	0.0000
Hutchinson Isl., Florida, U.S.A.	424	0	0.0525 - 0.0275	0.1667	0.4237
Quintana Roo, Mexico	100-400	565			
Totals	9974–29,924		n = 6 populations	n = 6 populations	

ferences between the east central Florida juvenile foraging population and the Nicaraguan adult foraging population in both haplotype composition and ML estimates of contributions by source populations. There are also significant differences between east central Florida and the Bahamian juvenile foraging population, but there are no significant differences between the Nicaraguan adult foraging population and the Bahamian juvenile foraging population. In all mixed stock analyses, the same source populations were used to estimate composition of the foraging populations.

The difference between the Nicaraguan adult foraging population and the Florida juvenile population is not surprising because these two populations represent different developmental stages in green turtles; however the significant difference between the two juvenile foraging populations is unexpected. The estimated composition of the east central Florida foraging population of juvenile green turtles is 53% Costa Rican and 42% Florida/Mexico, and comparable estimates for the Bahamian juvenile population consist of 80% Costa Rican and 14% Aves/Surinam (Lahanas et al., 1998). This difference in composition between the Bahamas and Florida foraging populations is puzzling considering their close proximity to each other and similar size classes: Bahamas, 31-67 cm (Lahanas et al., 1998) and Florida, 25-70 cm. The differences in foraging ground composition could be attributed to the proximity of potential contributing nesting populations or various combinations of dispersal mechanisms. In this analysis, it appears that the proximity of a nesting location to a foraging location may be more important than the size of the nesting population. Whether this is a general feature of green turtle life history or a characteristic of coastal Florida populations remains to be seen.

The difference between Florida and Bahamas may be due to temporal sampling effects. Sampling over a short time frame and from one season would not allow detection of changes in haplotype composition over time. If interyear or interseason variation in demographic composition is

extensive, synoptic sampling during one season would give an indication of the composition for only that time interval. Pooling samples from several years without testing for sample differences may provide misleading conclusions regarding the "typical" composition of a foraging ground population. Additionally, pooling samples among years will not allow the detection of other factors that may influence recruitment to a given foraging location.

Many factors could influence temporal variation including known differences in nesting density from year to year and hatch success rates. Environmental factors related to climate probably influence hatch success for a given nesting season and therefore alter the number of juveniles recruiting to a given foraging area. Weather can also affect water current patterns and thereby the location of juveniles when they switch to coastal benthic feeding.

The possibility of innate or heritable differences in habitat preference between nesting colonies cannot be excluded. Adult female marine turtles return to a specific location to nest, and evidence from molecular studies indicates that they are using natal homing to arrive at these locations (Bowen et al., 1989). Other marine animals are known to migrate to locations that they have never actually experienced; the American eel, Anguilla rostrata, spawns in the Sargasso Sea (Helfman et al., 1997) and leptocephalus larvae eventually recruit to North American streams and rivers draining into the Atlantic. Upon reaching sexual maturity, eels migrate back to the Sargasso Sea, a location they last inhabited as an egg or newly hatched larvae. Such examples caution researchers not to underestimate the potential sophistication of genetically programmed behaviors.

Transport routes for hatchlings are probably influenced strongly by oceanic currents (Carr, 1987; Collard and Ogren, 1990; Witham, 1991). Carr (1987) hypothesized that loggerhead turtle (Caretta caretta) offspring from the eastern North American nesting populations became entrained in the Gulf Stream and are passively transported across the North Atlantic. The North Atlantic gyre may eventu-

ally transport 30–40 cm individuals back to the western Atlantic. Recent genetic work by Bolten et al. (1998) provided evidence in support of Carr's hypothesis and the important role of oceanic currents in early loggerhead life history. We suspect that there are similar influences on the distribution of juvenile green turtles. Coastal and oceanic currents undoubtedly act as passive transportation routes (Carr and Meylan, 1980) and/or barriers. The Florida Current lies between the Florida and Bahamaian foraging grounds and may serve as a barrier to post-hatchling juveniles, potentially reducing the opportunities for animals to move into fertile Bahamian feeding areas. The role that these currents play in the determination of migratory routes for pelagic juveniles is difficult to evaluate or incorporate into models for predicting the composition of foraging grounds, yet it seems reasonable that the contribution is significant. For example, juveniles could encounter the Florida current and drift along, foraging in the sargassum as has been observed in the western Caribbean (Carr and Meylan, 1980). At some time, they may drop out in foraging areas such as the Core or Pamlico Sounds in North Carolina or continue along further north and follow the same currents as juvenile loggerheads.

A final possibility, which encompasses elements of both genetic programming and oceanic currents, is that (1) juveniles are randomly delivered to foraging locations by the aforementioned currents and (2) as they mature at a particular foraging location, hormonal changes may cause animals to move toward their natal beaches. Owens (1997) proposed a transition away from temperature-related androgen cycles to a photo-period related cycle. This initiation of a photo-period related cycle coincides with the transition to the final developmental foraging habitat from which adults will make their reproductive migrations.

Developmental Habitats

It has been suggested that there are two groups of immature green turtles on the east central Florida coast, based on mean

carapace length; smaller turtles inhabiting sabellariid worm reefs and the larger (but still immature) turtles inhabiting the Indian River lagoon (Ehrhart, 1983; Guseman and Ehrhart, 1990). Small green turtles captured by the power plant are apparently associated with nearshore reef habitat. These reefs are hypothesized to be an important intermediate developmental habitat between the pelagic and adjacent lagoonal stages of development (Guseman and Ehrhart, 1990). Tagging studies by researchers at the St. Lucie power plant support this hypothesis and indicate that there is some movement of turtles between the power plant and the Indian River lagoon system (J. Gorham, personal communication). Genetic markers would be useful to test this observation and make a link between developmental habitats. Studies are presently being conducted to examine the composition of juvenile foraging populations in both the reef and lagoonal developmental habitats (D. Bagley, personal communication). The dispersal of larger turtles from the Indian River lagoon system to sub-adult foraging grounds is largely unknown, but it has been suggested that these sub-adult turtles are highly migratory (Witham, 1991). Tagging at the power plant supports this hypothesis and indicates that the green turtles from east central Florida disperse over a wide geographic area that includes the east coast of the U.S.A. to Central America (J. Gorham, personal communication).

Management Implications

The fact that turtles from genetically distinct stocks share coastal and pelagic developmental habitats may raise doubts regarding the effectiveness of conservation strategies based on geographical or political boundaries (Bowen and Witzell, 1996; Carr and Stancyk, 1975). Turtles hatched in Central and South America or the Caribbean Islands may spend their early "lost" years in the oceanic pelagic environment. As juveniles and subadults, they may settle on coastal reefs 1000s of kilometers away from their country of natal origin, eventually establishing themselves in adult foraging and reproductive habitats in yet

another jurisdiction. Clearly, international recovery programs that protect turtles throughout their life cycle must be strengthened. In support of this effort, turtles need to be sampled from major developmental habitats in order to determine population origin and the movements of all life history stages. In the case of the green turtle, we must recognize the potential impact that mortality during juvenile stages in waters of the U.S.A. will have on the nesting populations utilizing beaches in widespread countries such as Mexico, Costa Rica, Venezuela, and Surinam.

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LITERATURE CITED

- ALLARD, M. W., M. M. MIYAMOTO, K. A. BJORNDAL, A. B. BOLTEN, AND B. W. BOWEN. 1994. Support for natal homing in green turtles from mitochondrial DNA sequences. Copeia 1994:34–41.
- BASS, A. L. 1999. Genetic analysis to elucidate the natural history and behavior of hawksbill turtles (*Eretmochelys imbricata*) in the wider Caribbean: a review and re-analysis. Chelonian Conservation and Biology 3:195–199.
- BASS, A. L., C. J. LAGUEUX, AND B. W. BOWEN. 1998. Origin of green turtles, *Chelonia mydas*, at "sleeping rocks" off the northeast coast of Nicaragua. Copeia 1998:1064–1069.
- BOLTEN, A. B., K. A. BJORNDAL, H. R. MARTINS, T. DELLINGER, M. J. BISCOITO, S. E. ENCALADA, AND B. W. BOWEN. 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. Ecological Applications 8:1–7.
- BOWEN, B. W., F. A. ABREU-GROBOIS, G. H. BALAZS, N. KAMEZAKI, C. J. LIMPUS, AND R. J. FERL. 1995. Trans-Pacific migrations of the loggerhead sea turtle demonstrated with mitochondrial DNA mark-

- ers. Proceedings of the National Academy of Sciences USA. 92:3731–3734.
- BOWEN, B. W., A. B. MEYLAN, AND J. C. AVISE. 1989. An odyssey of the green turtle: Ascension Island revisited. Proceedings of the National Academy of Sciences USA. 86:573–576.
- BOWEN, B. W., AND W. N. WITZELL. 1996. Sea turtle conservation genetics. Pp. 1–7. In B. W. Bowen and W. N. Witzell (Eds.), Proceedings of the International Symposium on Sea Turtle Conservation Genetics. NOAA Technical Memorandum, NMFS-SEFSC-396, Miami, Florida, U.S.A.
- BRODERICK, D., C. MORITZ, J. D. MILLER, M. GUINEA, R. J. PRINCE, AND C. J. LIMPUS. 1994. Genetic studies of the hawksbill turtle *Eretmochelys imbricata*: evidence for multiple stocks in Australian waters. Pacific Conservation Biology 1:123–131.
- CARR, A. 1987. New perspectives on the pelagic stage of sea turtle development. Conservation Biology 1: 103–121.
- CARR, A., M. H. CARR, AND A. B. MEYLAN. 1978. The ecology and migrations of sea turtles, 7. The west Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162:1–46.
- CARR, A., AND A. B. MEYLAN. 1980. Evidence of passive migration of green turtle hatchlings in sargassum. Copeia 1980:366–368.
- CARR, A., AND L. OGREN. 1960. The ecology and migrations of sea turtles, 4. The green turtle in the Caribbean Sea. Bulletin of the American Museum of Natural History. 121:6–48.
- CARR, A., AND S. STANCYK. 1975. Observations on the ecology and survival outlook of the hawksbill turtle. Biological Conservation 8:161–172.
- CHALOUPKA, M. Y., AND J. A. MUSICK. 1997. Age, growth, and population dynamics. Pp. 233–276. In P. L. Lutz and J. A. Musick (Eds.), The Biology of Sea Turtles. CRC Press, Boca Raton, Florida, U.S.A.
- COLLARD, S. B., AND L. H. OGREN. 1990. Dispersal scenarios for pelagic post-hatchling sea turtles. Bulletin of Marine Science 47:233–243.
- DERANIYAGALA, P. E. P. 1939. The tetrapod reptiles of Ceylon. Ceylon Journal of Science 1:1–242.
- DODD, C. K. 1982. Nesting of the green turtle, Chelonia mydas (L.), in Florida: historic review and present trends. Brimleyana 7:39–54.
- EĤRHART, L. M. 1983. Marine turtles of the Indian River lagoon system. Florida Scientist 46:337–346.
- EHRHART, L. M., AND P. W. RAYMOND. 1987. Loggerhead turtle, *Caretta caretta*, and green turtle, *Chelonia mydas*, nesting densities in south Brevard County, Florida, 1981–1984. Pp. 21–25. *In* W. N. Witzell (Ed.), Ecology of East Florida Sea Turtles. NOAA Technical Report, National Marine Fisheries Service 53, Miami, Florida, U.S.A.
- ENCALADA, S. E., P. N. LAHANAS, K. A. BJORNDAL, A. B. BOLTEN, M. M. MIYAMOTO, AND B. W. BOW-EN. 1996. Phylogeography and population structure of the Atlantic and Mediterranean green turtle *Chelonia mydas*: a mitochondrial DNA control region sequence assessment. Molecular Ecology 5: 473–483
- ERNEST, R. G., R. E. MARTIN, N. WILLIAMS-WALLS,

- AND J. R. WILCOX. 1989. Population dynamics of sea turtles utilizing shallow coastal waters off Hutchinson Island, Florida. Pp. 57–59. *In* S. A. Eckert, K. L. Eckert, and T. H. Richardson (Compilers), Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum, NMFS-SEFC-232, Miami, Florida, U.S.A.
- FELSENSTEIN J. 1993. PHYLIP: Phylogenetic inference package, version 3.5c. Department of Genetics, University of Washington, Seattle, Washington, U.S.A.
- GRANT, W. S., G. B. MILNER, P. KRASNOWSKI, AND F. M. UTTER. 1980. Use of biochemical genetic variants for identification of sockeye salmon (Oncorrhynchus nerka) stocks in Cook Inlet, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 37:1236–1247.
- GUSEMAN, J. L., AND L. M. EHRHART. 1990. Green turtles on sabellariid worm reefs: initial results from studies on the Florida Atlantic coast. Pp. 125–127. In T. H. Richardson, J. L. Richardson, and M. Donnelley (Compilers), Proceedings of the Tenth Annual Workshop on Sea Turtle Conservation and Biology. NOAA Technical Memorandum, NMFS-SEFC-278, Miami, Florida, U.S.A.
- HELFMAN, G. S., B. B. COLLETTE, AND D. E. FACEY. 1997. The Diversity of Fishes. Blackwell Science, Malden, Massachusetts, U.S.A.
- HILLIS, D. M., B. K. MABLE, A. LARSON, S. K. DAVIS, AND E. A. ZIMMER. 1996. Nucleic acids IV: Sequencing and cloning. Pp. 321–381. In D. M. Hillis, C. Moritz, and B. K. Mable (Eds.), Molecular Systematics, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, U.S.A.
- INNIS, M. A., D. H. GELFAND, J. J. SNINSKY, AND T. J. WHITE. 1990. PCR Protocols: a Guide to Methods and Applications. Academic Press, San Diego, California, U.S.A.
- LAHANAS, P. N., K. A. BJORNDAL, A. B. BOLTEN, S. E. ENCALADA, M. M. MIYAMOTO, R. A. VALVERDE, AND B. W. BOWEN. 1998. Genetic composition of a green turtle feeding ground population: evidence for multiple origins. Marine Biology 130:345–352.
- LAURENT, L., P. CASALE, M. N. BRADAI, B. J. GOD-LEY, G. GEROSA, A. C. BRODERICK, W. SCHROTH, B. SCHIERWATER, A. M. LEVY, D. FREGGI, E. M. ABD EL-MAWLA, D. A. HADOUD, H. E. GOMATI, M. DOMINGO, M. HADJICHRISTOPHOSOU, L. KOR-NARAKY, F. DEMIRAYAK, AND C. H. GAUTIER. 1998. Molecular resolution of marine turtle stock composition in fishery bycatch: a case study in the Mediterranean. Molecular Ecology 7:1529–1542.
- LEGENDRE, P., AND A. VAUDOR. 1991. The R Package: Multidimensional Analysis, Spatial Analysis. Département de sciences biologiques, Université de Montréal, Montréal, Canada.
- MARTIN, R. E., R. G. ERNEST, N. WILLIAMS-WALLS, AND J. R. WILCOX. 1989. Size distribution and seasonal abundance of loggerhead and green turtles in nearshore waters off Hutchinson Island, Florida. Pp. 334–335. In L. Ogren (Ed.), Proceedings of the Second Annual Western Atlantic Turtle Symposium. NOAA Technical Memorandum, NMFS-SEFC-226, Miami, Florida, U.S.A.

- MASUDA, M., S. NELSON, AND J. PELLA. 1991. User manual for GIRLSEM, GIRLSYM, and CONSQRT. USA-DOC-NOAA-NMFS. [Programs and user manual available from US-Canada Salmon Program, 11305 Glacier Highway, Juneau, Alaska 99801, USA.]
- MENDONÇA, M. T. 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Copeia 1983:1013–23.
- MENDONÇA, M. T., AND L. M. EHRHART. 1982. Activity, population size and structure of immature *Chelonia mydas* and *Caretta caretta* in Mosquito lagoon, Florida. Copeia 1982:161–167.
- MEYLAN, A., B. SCHROEDER, AND A. MOSIER. 1995. Sea turtle nesting activity in the state of Florida 1979–1992. Florida Marine Research Publications 52:1–51.
- MILLER, J. D. 1997. Reproduction in sea turtles. Pp. 51–81. In P. L. Lutz and J. A. Musick (Eds.), The Biology of Sea Turtles. CRC Press, Boca Raton, Florida, U.S.A.
- MULLIS, K. B., AND F. FALOONA. 1987. Specific synthesis of DNA in vitro via polymerase-catalyzed chain reaction. Methods in Enzymology 155:335–350.
- MUSICK, J. A., AND C. J. LIMPUS. 1997. Habitat utilization and migration in juvenile sea turtles. Pp. 137–163. *In* P. L. Lutz and J. A. Musick (Eds.), The Biology of Sea Turtles. CRC Press, Boca Raton, Florida, U.S.A.
- OWENS, D. W. 1997. Hormones in the life history of sea turtles. Pp. 315–341. In P. L. Lutz and J. A. Musick (Eds.), The Biology of Sea Turtles. CRC Press, Boca Raton, Florida, U.S.A.
- PELLA, J. J., AND G. B. MILNER. 1987. Use of genetic marks in stock composition analysis. Pp. 247–276. In N. Ryman and F. Utter (Eds.), Population Genetics and Fisheries Management. University of Washington Press, Seattle, Washington, U.S.A.
- PROFFITT, C. E., R. E. MARTIN, R. G. ERNEST, B. J. GRANUNKE, S. E. LECROY, K. A. MULDOON, B. D. PEERY, J. R. WILCOX, AND N. WILLIAMS-WALLS. 1986. Effects of power plant construction and operation on the nesting of the loggerhead sea turtles (Caretta caretta): 1971–1984. Copeia 1986:813–816.
- RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.
- ROFF, D. A., AND P. BENTZEN. 1989. The statistical analysis of mitochondrial DNA polymorphisms: chi-square and the problem of small samples. Molecular Biology and Evolution 6:539–545.
- TRUE, F. W. 1887. The turtle and terrapin fisheries. Pp. 493–503. In G. B. Goode (Ed.), The Fisheries and Fishery Industries of the United States. Sec. 5, Vol. 2, pt. XIX, U.S. Commercial Fisheries, Government Printing Office, Washington, D.C., U.S.A.
- WILCOX, W. A. 1898. Commercial fisheries of the Indian River, Florida. Report to the U.S. Commercial Fisheries 22:249–262.
- WILLIAMS-WALLS, N., J. O'HARA, R. M. GALLAGHER, D. F. WORTH, B. D. PEERY, AND J. R. WILCOX. 1983. Spatial and temporal trends of sea turtle nesting on Hutchinson island, Florida, 1971–1979. Bulletin of Marine Science 33:55–66.
- WITHAM, R. 1991. On the ecology of young sea turtles. Florida Scientist 54:179–180.

WITHERINGTON, B. E., AND L. M. EHRHART. 1989. Hypothermic stunning and mortality of marine turtles in the Indian River lagoon system, Florida. Copeia 1989:696–703.
WITZELL, W. N. 1994. The origin, evolution, and demise of the U.S. sea turtle fisheries. Marine Fisheries Region 56:8, 23

eries Review 56:8-23.

ZAYKIN, D. V., AND A. I. PUDOVKIN. 1993. Two programs to estimate significance of χ^2 values using pseudo-probability tests. Journal of Heredity 84:152.

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